ON THE STRUCTURE AND CLASSIFICATION OF THE MESOZOIC MAMMALIA.

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[ABSTRACT.]

This paper is an outline of the writer's observations upon the structure of the British Mesozoic Mammals and a classification of the Mesozoic Mammals in general, in view of their relationship to each other and to recent orders.

When Professor Owen completed his Memoir[1] in 1871 there were but twenty genera of pre-Tertiary Mammals known to science. Discoveries in the Mesozoic strata of Germany,[2] South Africa[3] and North America[4] have now increased this number to over forty genera, five of which are from the Upper Triassic, the remainder from the upper and lower Jurassic, and one from the Cretaceous.[5] Successors of the Mesozoic mammals have been discovered at the bottom of the American Eocene[6] and in the lower French Eocene Beds.[7] Among the latter are mammals which clearly connect upper Triassic[8] with Quaternary genera.[9] Through the kindness of the members of the Geological Department of the British Museum I was recently enabled to study the British types very carefully, and, enjoying soon afterwards an examination of the fine collections of Professor Marsh and Professor Cope,[10] I have been able to compare the type specimens of all the Mesozoic mammals, with the exception of four genera.[11] The most striking result of this comparison is the

1. Monograph of the Fossil Mammalia of the Mesozoic Formations, Palaeontographical Society, 1871.

2. *Triglyphus*, discovered by Prof. Fraas in the Rhaetic Beds near Stuttgart.

3. *Tritylodon*, from the Stormberg Beds, Upper Triassic, South Africa.

4. Numerous genera discovered by Prof. Marsh in the Atlantosaurus Beds parallel with the English Purbeck.

5. *Meniscoëssus*, described by Professor Cope, from the Laramie Beds.

6. I refer to Professor Cope's genera *Polymastodon*, *Chirox* and *Ptilodus*.

7. The *Plagiaulax* group, discovered by Dr. Lemoine at Rheims.

8. *Microlestes* and 9 *Thylacoleo* are united by the intermediate *Plagiaulacidae*.

10. This assistance will be more fully acknowledged elsewhere. I am especially indebted to Mr. Richard Lydekker for much valuable assistance.

11. *Stereognathus*, *Amphilestes*, *Triglyphus*, *Microlestes antiquus* (Plieninger's type specimen.)

Full acknowledgement will be made later of the use made of the valuable suggestions of Professor Owen and other writers.

close structural similarity between genera from widely separate localities, and the absence of types which are wholly distinct from the British, even in this greatly extended field of exploration. In other words, the Mesozoic genera appear to have had a very wide geographical distribution, and many scattered forms, while generically distinct, are closely connected by family and ordinal characters. The second result, which has been attained much more slowly, is that these mammals, with a few exceptions, can now be provisionally classified, as they fall into small groups with carnivorous, omnivorous, insectivorous, and herbivorous dentition, each with clearly marked characters. The third result which rests upon more debatable grounds is, that while many of these Mesozoic families became extinct in succeeding geological periods, many others belong in or near the ancestral lines of families still existing among the Marsupials and Insectivores.

Before entering the subject of classification I will give a brief resumè of my observations upon the British genera in so far as they differ from, or are additional to those of Professor Owen. It appears, from the dentition of a mandibular ramus belonging to *Amphitherium* which has been recently added to the British Museum collection, that three distinct genera have hitherto been included under this genus, which may be separated by the number of premolars, by the conformation of the molar crowns and the form and positions of the condyle, as *Amphitherium*, *Amphitylus* and *Amphilestes*.[1] (2) *Phascolotherium*. The formula is i 4 c 1 pm 0 m 7. It seems more probable that this genus has lost its premolars, (which formerly may have filled the diastema), than that they should all have become molariform, a modification which is always slowly acquired. (3) *Triconodon*. The upper canine of this genus has a double fang. The most interesting fact brought out is the evidence the various specimens furnish of relationship to the Marsupials in the succession of the teeth.[2] The fully adult molar formula is pm 4 m 4. The fourth

1. The *Amphitherium* (A. Prevostii) molar is bicuspidate with a low posterior heel. The *Amphitylus* (*gen. nov.*) molar has three blunt cusps, and an internal cingulum; form, *pm* 6, *m* 6. The *Amphilestes* molar has three prominent cusps and a pronounced cingulum, encircling the crown; *pm* 5, *m* 6. After a personal examination of the types, Mr. Lydekker writes me (April 16th) that he finds the formulae of both *Amphilestes* and *Amphitylus*, as follows: *i* 4 *c* 1 *pm* 4 *m* 7.

2, Assisted by Mr. Lydekker, I have confirmed the suggestions of Professor Owen and Professor Flower.

premolar early replaces a *molariform milk* tooth d_4 and the fourth true molar is very late in coming in. *Triacanthodon* is thus a synonym of *Triconodon*. (4) *Phascolestes*. There is no doubt that this genus is distinct from *Peralestes*,[3] but it is a question whether the type mandible does not belong to a genus near *Stylodon*. Form. i 4 c 1 pm 4 m 8. (5) *Leptocladus*, is widely separate from *Stylodon*.[4] Its molars, with single recurved cusps and elevated heels are wholly unique. The post-canine formula was probably pm 4 m 6. (6) *Peramus* is also widely separated from other genera in its dental formula, pm 6 m 3; all other polyprotodont genera of this period having four or more molars. The teeth in the type of this genus are seen upon the outer surface only. It is probable that when the inner surface is known, the formula will be modified to pm 4 m 5. (7) In the genus *Spalacotherium* the molars and premolars are well differentiated; the formula is i ? 2, c 1, pm 4, m 6. (8) *Peralestes* probably has a closely related form in *Peraspalax*, in fact the generic distinctness of the latter is doubtful. The post-canine formulæ are, *Peralestes* pm 5 m 6; *Peraspalax*, pm 4, m 7. (9) The maxilla which was referred to the genus *Stylodon* by Professor Owen, must be removed to a distinct genus, *Athrodon*, characterized by the compact position and peculiar wearing pattern of the crowns. (10) The maxillary formula of *Bolodon* is found to be i ? 2, c 0, pm 3, m 4. The characters of these teeth are clearly shown in the accompanying cut.

Leaving out of view for the present, all consideration of relationships to recent forms, we find that the Mesozoic Mammalia divide into two larger groups. In the first group (I) one of the incisors is greatly developed at the expense of the others and of the canine; there is a diastema varying in width in front of the first premolar and the true molars are invariably characterized by two or more antero-posterior rows of tubercles separated by longitudinal valleys or grooves. For this group we may adopt the sub-order *Multituberculata*, proposed by Professor Cope.[5]

The second group (II) does not show such close internal relationship among its members as does the foregoing, but is well separated from it by such characters as the following:

The incisors are numerous and subequal in size, the canines are

3. Professor Owen separated this genus doubtfully from *Peralestes*.

4. Professor Owen placed it doubtfully near this genus.

5. American Naturalist, 1884, p. 687.

large; there is usually no diastema, the premolar-molar series are usually in excess of the typical number and the molars are cusped rather than tubercular. If we were sure of the marsupial relationship of the members of this group we might place them with the sub-order *Polyprotodonta*, but some of the included families belong near the Insectivora.

I. Multituberculata.

(1) *Plagiaulacidæ.* This is probably the oldest family of this group and is well characterized by the laterally compressed trenchant premolars. The molars of *Microlestes antiquus* of Plieninger are essentially similar to those of *Plagiaulax*. The *M. Moorei* molars cannot be distinguished generically from those of *Plagiaulax*.[6] The least specialized *Plagiaulax* is *Ctenacodon*, Marsh.[1] The modifications in this family are well known as witnessed in the series *Plagiaulax, Ptilodus, Neoplagiaulax.*

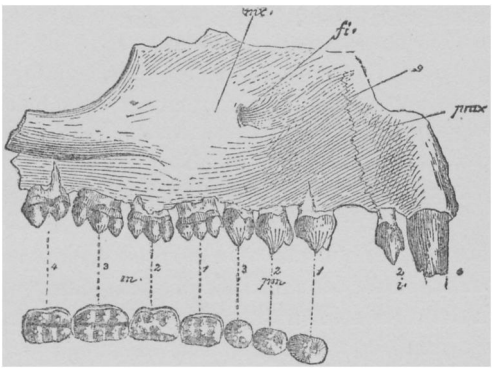

Fig. 1. Right Maxilla of Bolodon.

(2) *Bolodontidæ.* This family includes *Bolodon* and *Allodon* Marsh.[2] The premolars are not trenchant. The molars have two straight rows of conical tubercles separated by a longitudinal valley. Although allied to the *Plagiaulacidæ* we cannot place these genera in this family because the molar pattern is essentially different.

6. The molars of *M. Antiquus, M. Moorei* and *P. Minor* in each case show a closely similar disposition of the tubercles.

1. Am. Journ. Sc. and Arts, Nov. 1879, p. 238.

2. This genus is very close to *Bolodon* in all the details of tooth structure, but shows the alveolus of a small median incisor which may be wanting in *Bolodon*. *Allodon* has been placed in the Plagiaulacidae by Professor Marsh, Am. Journ. Sc. and Arts, April 1887, p. 329.

Bolodon has conical tubercular instead of trenchant premolars. In *Plagiaulax* the tubercles are irregular crenations of the border of the basin shaped crown. In *Bolodon* they are minute, sharply defined cones arranged in straight rows with a deeply worn groove between them; this pattern is like that of *Tritylodon* with two rows of tubercles instead of three.

The general likeness between *Bolodon* and *Tritylodon* is very striking in spite of the great discrepancy in size. The latter genus is perhaps synonymous with *Triglyphus*[4] (Fraas) and forms the type of the family (3) *Tritylodontidae*[1] (Cope), characterized by the absence of trenchant premolars and the presence of upper molars with three parallel rows of tubercles separated by grooves. The *Polymastodontidæ* (Cope) forms a fourth, more recent family[1].

The position of *Stereognathus*, *Chirox* and *Meniscoëssus* is uncertain, although they probably belong to this Sub-Order. *Meniscœssus* stands nearest the *Plagiaulacidae*, and *Chirox* intermediate between the *Bolodontidae* and *Tritylodontidae*.

II. Second Group.

1. JURASSIC MAMMALS.

Among the second group of mammals I find that the molar pattern forms an advantageous starting point for classification. Contrary to the usual statement, the premolars are invariably unlike the molars[2], but the whole dental series, as well as the mandible, are in a marked degree correlative in structure and in most instances distinctly specialized for certain kinds of diet. Some of the molar patterns with the correlated structures, prevail in a number of genera which we may group in a family, without knowing exactly where to place it in the zoölogical scale. The molars of other genera are transitional in structure between two distinct types. Other genera again are entirely isolated in their molar structure where no allied forms have been discovered. This classification by families is, of course, a temporary one, subject to change as the genera become more fully known. The *Stylodontidae* form the only fully defined family.

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4. See Neumayr. Neues Jahrbuch für Min. u. Pal. 1884, p. 279.

1. Am. Naturalist, 1884.

2. *Phascolotherium* forms an apparent but not real exception, since the premolars have probably disappeared. In *Diplocynodon*, (Marsh, loc. cit. Plate x), the premolars when viewed upon the inner surface are very distinct from the molars.

The chief molar types which characterize families are as follows:

A. Without opposition of cusps. (1) With three stout, erect cusps in line. (2) Transitional. With three cusps not in line, two being rotated inwards. (3) With three slender, divergent cusps in line. *B. With completely opposed cusps, separated by a longitudinal valley.* (4) *C. With completely opposed cusps connected by transverse ridges.* (5) Molars with a single styloid cusp on one side of the crown connected by divergent ridges with a pair of cusps on the other side. *D. Without cusps.* (6) The crowns columnar, with a smooth wearing surface.

By a careful study of the dentition and mandibular structure, we find that these families unite in small groups which are *in early stages of differentiation along certain lines of functional adaptation.* These lines are not sharply defined, but by a comparison of the typical forms with the most nearly allied genera of known adaptation I find we may divide these sub-groups into carnivorous, omnivorous insectivorous and herbivorous series; employing these terms in a broad sense as indicating an initial rather than an advanced specialization of structure.

Carnivorous Sub-Group.

There are many points of resemblance between the following three families, although at first sight they differ widely. They mostly embrace the largest genera and the teeth are generally adapted to a carnivorous diet, especially in the first and second families; in the third there is an apparent divergence towards another type of dentition and function. The molars have a strong internal cingulum. The premolars have basal cusps. The condyle is low and the coronoid broad.

A. (1) *Triconodontidæ.*[1] The typical genus of this family is *Triconodon* (*syn. Triacanthodon*, Owen; *Priacodon*, Marsh.) The dentition is now fully known. There is no diastema. The premolars have strong basal cusps. The canines and the incisors are erect and powerful. The mandible is strong and the condyle is below the molar level. These characters and the likeness to *Thylacinus* show that this was a carnivorous animal. An older and much less specialized but probably allied form was *Amphilestes. Amphitylus* appears to be related by the character of its molars, but separated by its mandibular characters, as the condyle is high and pedunculate.

1. Proposed by Professor Marsh.

Amphitherium, on the other hand is allied by the structure of the

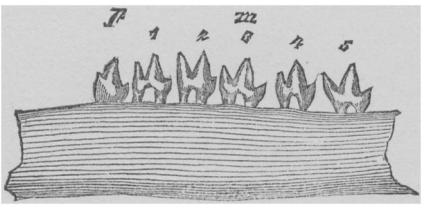

Fig. 2. Portion of the right mandible of Amphitherium.

mandible and separated by the pattern of the molars, which lack the third cusp. The last two genera are somewhat isolated.

(1*a*) An allied family is the *Phascolotheridae*[2] embracing *Phascolotherium* and *Tinodon*, in which there is a diastema behind the canine; true premolars are few or wanting[3], and the mandibular angle is represented merely by the inflection of the lower border. The molars are like those of the *Triconodontidae* except that the anterior and posterior cusps are smaller and are slightly rotated inwards.

(2) *Spalacotheridae*[1]. This family embraces *Spalacotherium* and *Menacodon*. The mandible is without a distinct angle, like that in *Phascolotherium*, but shallower and with a more elevated condyle. There is no diastema. The incisors and canines are somewhat similar to those of *Triconodon*. The premolars have strong anterior and posterior basal cusps. The anterior and posterior cusps of the molars are strongly rotated inwards.

Omnivorous Sub-Group.

B. The families embraced in this division are quite closely inter-related both as regards their dentition and diet. The genera vary from middle to large size. The typical forms (*Peralestidae*) were probably omnivorous. The incisors are not known, the canines are large and erect, the premolars have prominent basal cusps. Instead of an internal cingulum, the lower molars have a more or less prominent internal row of low cusps. The condyle is usually on or below the molar level.

2. This name is preferable to *Tinodontidae* recently proposed by Professor Marsh, since Prof. Owen's genus is much the best known. It is quite probable that the *Phascolotheridae* will be subsequently united with the *Triconodontidae*, linked by intermediate forms with premolars.

3. The post-canine teeth of *Tinodon* have not as yet been fully described.

1. This family name was proposed by Professor Marsh, loc. cit. p. 340.

The (4) *Peralestidae* embrace *Peralestes* and *Peraspalax* which are closely related if not synonymous. The lower premolars have distinct basal cups. The inner and outer molar cusps, instead of being united by a ridge as in the last, are separated by a longitudinal valley. The upper molars (*Peralestes*) have a lofty internal and several low external cusps, while the lower molars, (*Peraspalax*) have a high external and low internal cusps. The canines are strong. The lower molars are somewhat simpler but resemble those of *Dasyurus* and *Didelphys*. I infer that, like these modern marsupials, these animals were omnivorous.

The lower molars of the highly specialized genus *Paurodon*, the type of the *Paurodontidae* (Marsh), although fewer in number, are quite similar to those of *Peraspalax* and suggest an affiliation of these two families.

The *Diplocynodontidae* (Marsh) embrace *Diplocynodon*, *Docodon*, and *Enneodon*. The molars are transitional, illustrating the extension of the internal cingulum into a broad shelf leading towards a complete opposition of cusps such as we observe in *Peraspalax*, but it is as yet uncertain whether this family is affiliated to the *Peralestidae*. This family probably embraces Professor Owen's genus *Peramus*, in which the molar and mandibular structure is similar to that of *Diplocynodon*.

Insectivorous Sub-Group.

The two following families differ widely from those preceding. The genera vary from an extremely small to middle size. The teeth are adapted to an insectivorous diet, the incisors in the most typical forms being procumbent and spatulate, the canines small, the premolars lack distinct basal cusps, the last is lofty and pointed. The molars have no cingulum. The condyle is high and the coronoid slender. The formula is usually *pm* 4 *m* 8. The families are separated by the structure of the molars.[2]

(3) *Amblotheridae*. This embraces the genera *Achyrodon* and *Amblotherium*. The mandible is very slender and tapers to the symphysis, with a high condyle. The incisors are semi-procumbent and spatulate, the canines small, the last premolars very lofty

2. *Amblotherium* and *Achyrodon* are represented by mandibles seen upon the inner surface only. In the matrix impressions there is no evidence of outer cusps, but the teeth closely resemble those of the *Stylodontidae* as seen upon the inner surface, and these families may prove to be the same.

and without basal cusps, while the molars have no internal cingula and no opposition of cusps.

C. (5) *Stylodontidae*[1]. Thanks to the discoveries of Professor Marsh, this family is now very fully represented and the molar structure is well understood. It embraces *Stylodon* (Stylacodon)[2], *Aesthenodon, Laodon* and *Dryolestes* which is very similar to the genus *Phascolestes* (Owen.) There is little doubt therefore that the latter genus belongs here rather than near *Peralestes.* The resemblance of *Stylodon* to *Chrysochloris,* observed by Professor Owen, is very much strengthened by this extended knowledge of the *Stylodon* molars, and indicates that this family was insectivorous. The structure of the mandible is very similar to that of *Amblotherium.*

HERBIVOROUS SUB-GROUP.

D. The single family embraced in this division is widely separated from all which precede it. The structure of the molars indicates an herbivorous diet similar to that of the Rodents and the Wombats.

(6) *Athrodontidae. Athrodon*[3] is unique in its dentition among the Mesozoic mammals. The tall trihedral crowns are closely applied at their sides, thus falling into a curve. The inner face is styloid, while the outer is grooved and the triangular wearing surface is traversed by a faint median ridge, thus resembling one half the crown of a *Phascolomys* molar. The last premolar is transforming into a molar, the others are small. The canine is large and bifanged.

The genus *Leptocladus* is isolated.

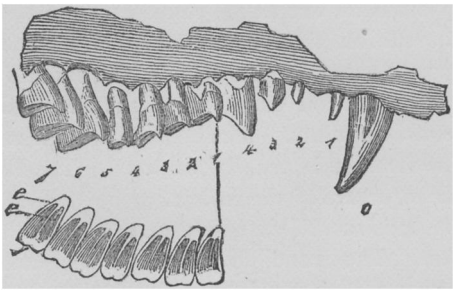

Fig. 3. The inner surface of the left maxilla of Athrodon.

1. This family name was suggested by Professor Marsh in 1880 to embrace *Stylodon* and *Stylacodon.* It is probably equivalent to the *Dryolestidae* more recently proposed by the same author.

2. These genera appear to be the same.

3. Gen. Nov. Type, maxilla of *Stylodon pusillus,* Owen.

Dromatherium is widely aberrant, and is the most reptilian in appearance of all the Mesozoic genera. Professor Marsh has proposed the family *Dromatheridae* to embrace this genus, but without defining it. Uniting it with *Microconodon*, the family may be characterized by the imperfect division of the fangs of the molars and the wide diastema behind the canine. The reptilian (Theromorph) condition of the molar fangs may be found to separate these genera still more widely from the jurassic forms so as to represent a new order of mammals, the *Protodonta*.

Conclusion.

It is now generally admitted that many of the genera embraced in the *Multituberculata* were Marsupials, and on many grounds it is safe to place this group as a Sub-Order of the Marsupialia. Are the Jurassic members of the second group also to be placed in this order or do they form a distinct order by themselves? Professor Marsh in his recent view of the Mesozoic mammals has held the latter view. It is, however, impossible to find a single common character[1] or set of characters for these genera which is of ordinal value. On the other hand, there are many grounds for placing the *Triconodontidae*, *Peralestidae* and *Athrodontidae*, and their affiliated families, in or near the ancestral lines of the modern *Dasyuridae* and *Phascolomidae* respectively, while the *Stylodontidae* are similarly related to the *Chrysochloridae*. These grounds may be partially stated. What holds good of one genus is naturally true of all the genera which are clearly allied to it. (1) *Triconodon* has one more premolar but otherwise resembles *Thylacinus* both in the structure of the mandible and in the form and succession of the teeth. (2) *Peraspalax*, although much more imperfectly known, is allied to *Dasyurus* in its molar structure. (3) *Athrodon*, although differing from *Phascolomys* in the possession of a large canine, shows a marked resemblance to this genus in the molar structure. We may designate the allied carnivorous, omnivorous and herbivorous sub-groups as proto-Marsupialia, a sub-order distinguished by the almost invariable presence of four premolars, a number unknown among modern Marsupials.

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1. The mylohyoid groove is universally present, but is also found in *Myrmecobius*.

In the *Amblotheridae* and *Stylodontidae* we probably have a line of Insectivora. (4) *Dryolestes* has a molar pattern which is not observed in any marsupial, but is seen in *Chrysochloris* among the Insectivora. Since, however, it is common for marsupials to mimic the dentition of other orders, this relationship must be held with some reserve.